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THE SENSE OF HEARING IN FISHES.[1]

G. H. PARKER.

THE sense of hearing is unusual in several respects. Unlike the other senses, it is restricted to comparatively few groups of animals; for, though many experiments have been tried, there is no conclusive evidence, so far as I know, that a sense of hearing is possessed by coral animals, jellyfishes, worms, starfishes, crabs, oysters, snails, and their allies. It is true that the older naturalists described for many of these animals organs that they called ear-sacs and that were supposed to act as organs of hearing, but the experimental work of the last fifteen years has shown that these organs are without doubt means of controlling the equilibrium of the animals, and not organs of hearing. The only animals in which a sense of hearing may be said without reservation to be present are the higher arthropods, particularly the insects, and the four higher classes of vertebrates, the amphibians, reptiles, birds, and mammals. Excepting the arthropods and the vertebrates, it seems probable that the other animals cannot hear, that while they may be influenced by contact with the world about them, by its light, its odors, etc., they are uninfluenced by its sounds; in other words, they live as though surrounded by perpetual silence.

The sense of hearing is not only restricted to a very few groups of animals, but the animals possessing it are always the more highly organized members of their groups. Thus, among the arthropods, a group which includes the crabs, lobsters, myriapods, spiders, and insects, the sense of hearing, if not absolutely restricted to the most highly organized class, the insects, is at least best developed in them. So, too, in the vertebrates, though the frogs, toads, turtles and their like have a sense of hearing, the efficiency of this sense is low compared with that which it attains in the birds and particularly in the mammals, the highest vertebrates. It is thus evident that the sense of hearing is coupled with high organization.

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When a survey of the whole animal kingdom is made, it is found that most sense organs are not restricted as the organs of hearing are; for instance, eyes, often of a complicated structure, occur in such lowly organized animals as jellyfishes, starfishes, and worms, and these animals react with great precision to light. Not only do many of these lower animals possess eyes, but they also have organs of touch, taste, etc.; in fact, the only important sense organ lacking in them is that of hearing. Since the sense of hearing is found only in the more highly organized animals and the other senses occur in the lower as well as in the higher animals, it follows that hearing is probably the most recently acquired of the senses.

If in accordance with these facts we endeavor to form some idea of the evolution of the sense organs in the animal series, we must picture to ourselves an early origin for all the important senses except hearing. This sense was undoubtedly the last important one to be differentiated and the reason for the lateness of its appearance I hope to make clear to you toward the close of this lecture.

It is a remarkable fact that the ear in the higher vertebrates, probably their latest important sensory acquisition, is an unusually perfect mechanism. Much has often been said about the perfection of the human eye and this organ undoubtedly displays a marvelously delicate construction, but in my opinion the efficiency of the ear as an organ of sense is as much beyond that of the eye as a modern chronometer is beyond an old-fashioned sundial. Evidence of the truth of this opinion can be seen in the many defects that are present in the eye as contrasted with the ear. For instance, what we call white light is well known to be any one of many possible mixtures of colored lights. Thus, when red light is combined with bluish green, the resultant is white; orange and sky-blue likewise produce white, as do also yellow and violet, green and pink, etc. To all these combinations, which are totally distinct from a physical standpoint, the eye answers with but one sign, that for white light.

Color in light corresponds to pitch in sound, for both depend upon wave lengths. Thus, the keys of a piano when struck in sequence give rise to a series of tones that differ one from another much as the colors of the spectrum do, namely, in the lengths of their waves. Although a trained eye cannot distinguish between white lights made by mixing different pairs of colored lights, even the unpracticed ear can distinguish between any pairs of tones when sounded on the keyboard, and, while the person may not be able to name the keys, the actual discrimination is easily accomplished. Thus white light is a measure of the deception due to our eyes, a deception that the ear ordinarily never gives rise to. Could we see the colors in ordinary light as we hear the tones in sound, the work of the most extreme French colorists would be dull in comparison with reality. The eye, therefore, fails to give much information about light that is obtained from the ear about sound.

The occurrence of well-developed organs of hearing only among the insects and higher vertebrates suggests, since these animals are air-inhabiting forms, that possibly the sense of hearing is capable of development only in an organism surrounded by air. To test this supposition one naturally turns to the nearest aquatic relatives of the groups possessing this sense. With the insects these relatives are probably the somewhat distantly related crustaceans, but with the vertebrates they are the fishes, a class closely allied to the other members of the vertebrate group. If the sense of hearing can originate only in air-inhabiting animals, no traces of it should be found among fishes. If it can arise in other situations, the fishes are probably the class in which its beginnings in the vertebrate series are to be sought for. The problem of hearing in fishes, therefore, is a general one dealing with the possible origin of one of the most important senses of vertebrates, a sense probably the most recently developed of all and yet in many respects the most efficient.

Hearing in fishes can best be approached from the standpoint of the human ear. The ear in man has long been known to be composed of three parts, the external, the middle, and the internal ear. The external ear consists of a complicated fold of skin known as the concha and a somewhat twisted tube leading inward to the ear-drum. The middle ear is a cavity in the head lying immediately internal to the ear-drum and connected with the mouth by the Eustachian tube. Through the cavity of the middle ear a bridge of small bones, the ear ossicles, passes from the ear-drum to the opposite wall of the middle ear where the innermost ossicle abuts against the cavity of the internal ear. The internal ear, which is situated somewhat deeper in the head than the middle ear, is a complicated fluid-filled sac with three semicircular canals and a spirally twisted portion, the cochlea. The nerve concerned with the sense of hearing ends in the walls of this sac. When the ear is normally stimulated, the sound-waves from the surrounding air beat against the ear-drum and set it in vibration. These vibrations cause the chain of ossicles to vibrate and thus the motion is handed on to the fluid of the internal ear. This fluid vibrates in turn and by some process not clearly ascertained stimulates the nerves on the walls of the ear-sac. As is well known the deafness caused by injuries to the external and the middle ear may often be relieved by various mechanical contrivances, but injuries to the internal ear are of an absolute kind and not open to amelioration, for the internal ear, as its nerve connections show, is the true organ of hearing, the middle and external ears being only means of conducting sound-waves to the true sense organ.

The form of ear just described is found only in the higher vertebrates; in the lower ones this organ presents a somewhat simpler structure. Thus, in the frog, there is no external ear, but the ear-drum is exposed directly on the surface of the head and the whole auditory apparatus consists of only the middle and the internal ear. In fishes a still further reduction takes place in that the middle ear as such is not developed. Thus the fishes possess only the essential part of the organ of hearing, the internal ear, and even this is in an altered form, for their ear-sacs, though complicated in outline and usually provided with three semicircular canals, lack almost all traces of the spirally twisted part, the cochlea.

That fishes possess a sense of hearing seems to have been generally admitted by the older observers. Thus Isaac Walton, in his "Complete Angler" (1653), when asked if trout can see at night replies "Yes, and hear and smell too." He then describes some experiments made by Sir Francis Bacon to show that sound can pass through water, experiments that led Walton to crave the pardon of one whom he had laughed at for affirming that carp would come to a certain place in a pond to be fed, at the ringing of a bell or the beating of a drum. He thereupon declares that "it shall be a rule for me to make as little noise as I can when I am fishing, until Sir Francis Bacon be confuted, which I shall give any man leave to do," and he finally resolves "to advise anglers to be patient and forbear swearing, lest they be heard, and catch no fish."

The internal ears of the higher fishes were also known to the older observers. So far as I am aware they were first described by Casserius in 1610 and were studied in some detail in the following century by Geoffroy, Scarpa, Comparetti and the celebrated British physician, Hunter. The attitude taken by many of these early workers in the question of the ability of fishes to hear is well illustrated by a quotation from a paper on the organ of hearing in fishes published by Hunter (1782). This paper contains the following statement (1782, p. 383): "As it is evident that fish possess the organ of hearing, it becomes unnecessary to make or relate any experiment, made with live fish which only tends to prove this fact; but I will mention one experiment, to shew that sound affects them much, and is one of their guards, as it is in other animals. In the year 1762, when I was in Portugal, I observed in a nobleman's garden, near Lisbon, a small fish-pond, full of different kinds of fish. Its bottom was level with the ground, and was made by forming a bank all round. There was a shrubbery close to it. Whilst I was laying on the bank, observing the fish swim about, I desired a gentleman, who was with me, to take a loaded gun, and go behind the shrubs and fire it. The reason for going behind the shrubs was, that there might not be the least reflection of light. The instant the report was made, the fish appeared to be all of one mind, for they vanished instantaneously into the mud at the bottom, raising as it were a cloud of mud. In about five minutes after they began to appear, till the whole came forth again."

This passage shows very clearly that in the opinion of Hunter the internal ears of fishes, like those of the higher vertebrates, are organs of hearing. Without further experimental evidence, this view was accepted by the celebrated physiologist Müller (1848, p. 1238) in his well-known chapters on the physiology of the senses, and by many other eminent authorities such as Owen (1866, pp. 342 and 346), Günther (1880, p. 116), and Romanes (1892, p. 250). To these investigators the presence of the internal ear, seemed, as it did to Hunter, sufficient ground for assuming that fishes could hear.

Within recent years, however, this opinion has been called in question or even denied. Some of the grounds for this change of view may be stated as follows. The English zoölogist Bateson (1890, p. 251) in some investigations on the sense organs and perception of fishes, observed that the report from the blasting of rocks caused congers to draw back a few inches, flatfishes like the sole, plaice, and turbot to bury themselves, and pouting to scatter momentarily in all directions. Other fishes seemed to take no notice of the report. When the side of a tank containing pollack or soles was struck with a heavy stick, the fishes behaved as they did toward the report of the blasting. Pollack did not respond, however to the sound made by rubbing a wet finger on the glass window of an aquarium or to the noise made by striking a piece of glass under water with a stone, provided the means of producing the noise was not seen by the fishes. Bateson concluded that, while it may be regarded as clear that fishes perceive the sound of sudden shocks and concussions when these are severe, they do not seem to hear the sounds of bodies moving in the water but not seen by them.

Without knowledge of Bateson's observations, the Viennese physiologist Kreidl (1895) carried out a series of experiments with the view of testing the powers of hearing in the goldfish. This species was chosen because of the ease with which it could be kept in the laboratory and further because it is one of those fishes that have long been reputed to come at the sound of a bell. After an extended series of experiments Kreidl (1895, p. 458) concluded that normal goldfish never respond to sounds produced either in the air or in the water, though they do react to the shock of a sudden blow given to the cover of the aqu rium. To test whether such responses were dependent upon the auditory nerves, Kreidl removed these nerves and the attached ear-sacs from a number of goldfishes and subjected them to stimulation by sound. In all cases they were found to respond precisely as the animals with ears did. Kreidl, therefore, concluded that goldfishes do not hear by the so-called ear, but that they react to sound waves by means of an especially developed skin sense, or, to put the matter in other words, the goldfish *feels* sound but does not *hear* it (Kreidl, 1896, p. 581). This condition is not so difficult to imagine as at first thought it seems, for we can not only hear sounds under water but we can also feel them, as anyone can prove by placing his hand under water near a loudly sounding body.

After Kreidl had reached his conclusion concerning goldfishes, he was led to take up a specific case of the response of fishes to the sound of a bell and an opportunity of doing this was found at the Benedictine monastery in Krems, Austria. Here the trout of a particular basin were said to come for food at the ringing of a bell. Kreidl (1896, p. 583), however, found that they would assemble at sight of a person and without the ringing of the bell. If they were not then fed, they soon dispersed and no amount of bell-ringing would induce them to return. If, however, a pebble or small piece of bread was thrown into the water, they immediately swam vigorously toward the spot where the disturbance had occurred. Moreover, if a person approached the basin without being seen and rang the bell vigorously, the fishes did not assemble. From these facts Kreidl (1896, p. 584) concluded that the assembling of the fishes was brought about through sight and the skin sense and not through hearing, and that the conclusion reached with the goldfish might be extended to other kinds of fishes.

While the problem of the auditory function of the ears of fishes was thus being investigated, a wholly different view as to the functions of these organs had been gradually opened up. Through the researches of Loeb (1888), Kreidl (1892), Bethe (1894), and Lee (1898) it became clear that whether the ears of fishes were auditory organs or not, they were, beyond doubt, organs for the control of the equilibrium of these animals, and in this respect they partook of the nature of the otocysts of the lower animals. My own few observations are fully in accord with this conclusion. When the nerves to the ears of the green killifish (Fundulus heteroclitus) are cut and the animal attempts rapid locomotion, it loses its bearings completely and swims in any position in spirals or even in circles. Thus the ear is in some way essential to the continued equilibrium of the fish. Although this conclusion has no direct bearing on the question of hearing in fishes, it makes it no longer necessary to assume that the presence of the internal ear in a given fish implies the ability of this fish to hear; hence the argument used by the older investigators is shown to be fallacious.

The conclusion arrived at by Kreidl that the ears of fishes like the goldfish, trout, etc. are not organs of hearing was supported and extended by the observations of one of our American physiologists, Dr. Lee of Columbia University, who studied the reactions of several species of fishes to such sounds as the human voice, the clapping of hands, and the striking of stones together in air and under water. In all his experiments Lee (1898, p. 137) obtained no evidence whatever of the existence of a sense of hearing as the term is usually employed; though he found that the fishes were exceedingly sensitive to gross shocks, such as the jarring of their tank or concussions upon its walls. From the observations and experiments of Bateson and of Kreidl and from his own work, Lee (1898, p. 138) believed that the conclusion is justified beyond doubt that fishes do not possess the power of hearing, in the sense in which the term is ordinarily used and that the sole function of the ear in fishes is equilibration. According to this view then, fishes resemble many of the lower aquatic animals, in that their so-called ears are not organs for hearing, but for controlling the equilibrium of their bodies; and, if they respond to sounds at all, they do so through the skin.

This general conclusion seemed to me not wholly in accord with certain well-known facts in the natural history of fishes. Most important of these is the undoubted ability on the part of some fishes to make sounds. Although it is conceivable that fishes, like some totally deaf persons, may produce vocal sounds that they themselves cannot hear, this conclusion is not probable and anyone that has ever heard a young swellfish (Chilomycterus schoepfi) make its characteristic sound when attacked by a hungry scup (Stenotomus chrysops) cannot but receive the impression that both fishes hear. Moreover it is very difficult without assuming hearing to understand the economy of sound production where, as in the squeteague or weakfish (Cynoscion regalis), this function is limited to one sex, in this instance the males. These habits raise the suspicion that notwithstanding the experimental evidence thus far brought forward, fishes may hear. It was chiefly because of this suspicion that last summer at the invitation of the United States Fish Commission I undertook to investigate this question.

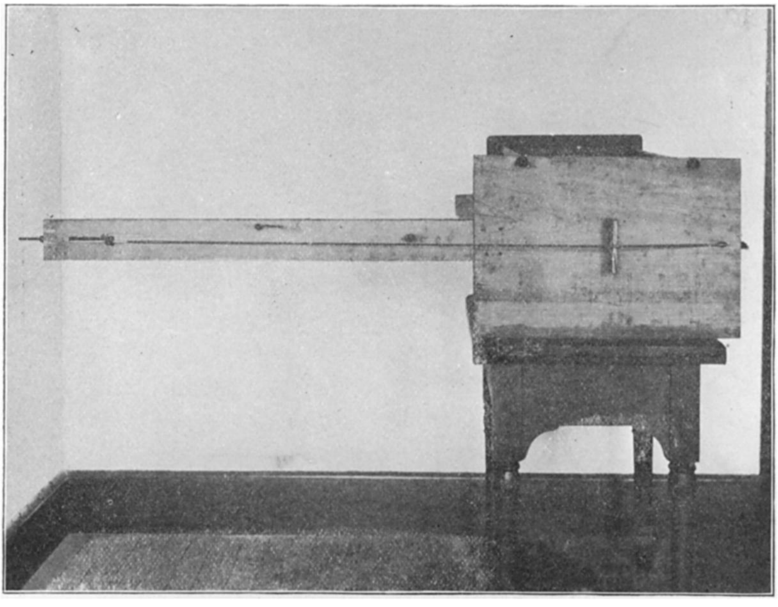

Fig. 1.

The apparatus used (Figs. 1 and 2) consisted of a large marine aquarium one end of which was replaced by a deal sounding board. On this board a bass viol string was stretched so that its vibrations could be transmitted through the board to the water in the aquarium. By frequent adjustment the string was kept at forty vibrations per second, corresponding to a tone almost as low as any used in music. Within the aquarium was suspended from distant supports a small glass cage for the retention of the fishes to be experimented upon. The end of the cage toward the sounding-board was open except for a fine net, which, though it restrained the fishes from escaping from the cage, made no serious interference with the entrance of sound.

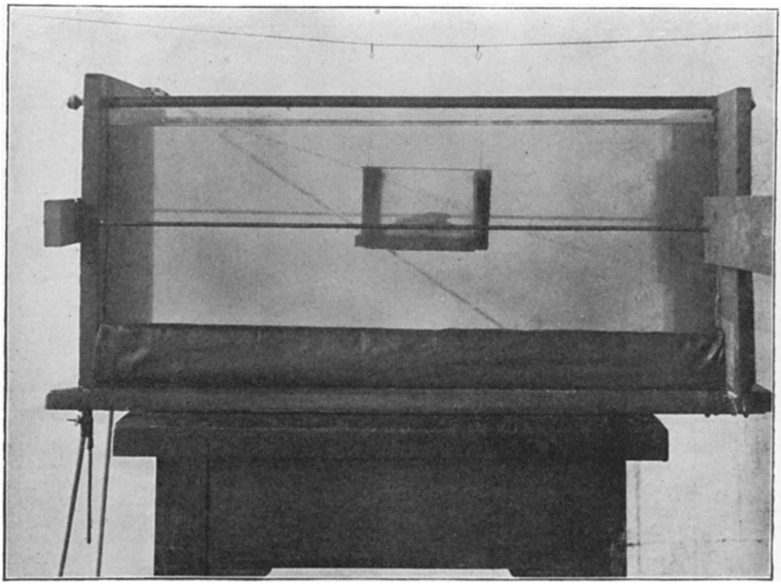

Fig. 2.

In testing fishes for the sense of hearing it must be evident from what has already been said that several precautions are necessary. First of all, the sounds used should be sustained and of relatively low intensity rather than of the kind that might produce a concussion or a shock. Next, care must be taken to determine whether these sounds influence the fish through its ears or through its skin; for if the ears are not stimulated, a sense of hearing cannot be said to be present. After some preliminary trials I finally resolved to use for my experiments the green killifish (Fundulus heteroclitus), a minnow common in the waters about the United States Fish Commission Station at Woods Hole, Massachusetts, where my work was done. This fish proved very hardy and in every way satisfactory for the work.

Three classes of killifishes were tested; first, those that were entirely normal; secondly, those in which the nerves to the ears had been cut; and, thirdly, those whose outer surfaces had been rendered insensitive by cutting the nerves to the skin. The fishes were easily etherized and cutting the nerves to the ears proved to be a simple though delicate operation. To render the skin insensitive, it was necessary to cut the fifth and seventh nerves, the lateral line nerves and the spinal cord, but from this apparently severe operation the fishes almost invariably recovered, fed well, and continued normally active for several weeks.

When a normal fish was placed in the cage and the bass viol string set in vibration, any one of four responses might be observed: first, the rate of the gill movements increased for a brief period; secondly, the pectoral fins, if quiet, were set in motion, or, if in motion, their rate was increased; thirdly, the tail fin often vibrated; and, finally, the whole fish might give a spring as if startled by the sound. Of these four reactions, the one most satisfactory for observation was the movement of the pectoral fins, and I subsequently used this almost exclusively in testing the fishes. Ten normal fishes when subjected each to ten tests with the sounding apparatus responded with the pectoral fins ninety-six times in the total hundred. This number may be taken as a basis of comparison for the fishes upon which operations had been performed.

To ascertain the importance of the ear in these responses, I next tested ten fishes in which the nerves to the ears had been cut and from ten observations on each fish I found that the number of responses to sound in a total of one hundred trials was only eighteen, and some of these eighteen were of doubtful character. It thus appears that cutting the nerves to the ears brings about a large reduction in the number of reactions and my results, therefore, are very different from those of Kreidl, who, it will be remembered, observed no difference in this respect between normal and earless goldfishes. Although at first sight it might seem that these experiments proved conclusively that the ear of the killifish is, if not the only organ of hearing, at least the chief organ for that sense, it is nevertheless conceivable that the reduction in the number of reactions shown by the earless fishes may be due not to the loss of the ear as a sense organ but to the severity of the operation that the fishes have undergone.

To determine how much weight should be given to this objection and at the same time to ascertain the part played by the skin in these reactions, I tested ten fishes in which the skin had been made insensitive but in which the ears were intact. In a total of one hundred trials, ten on each fish, there were ninety-four responses to sound and six failures; in other words, these fishes, though they had undergone more severe operations than the earless ones, reacted almost exactly as normal fishes did. These observations placed beyond a doubt the conclusion that the ears of the killifish are stimulated by the disturbances set up by the vibrating bass viol string, and the only question we have to answer before a final conclusion can be safely drawn is, whether these disturbances are really sound vibrations.

If the aquarium is observed closely when the bass viol string is made to vibrate, not only will a sound be heard but the whole aquarium will be seen to vibrate and ripples will be noticed passing over the surface of the water. Is it not possible that the fishes respond to the motion of the aquarium as a whole or to the disturbance indicated by the ripples rather than to the true sound-waves? To determine this point, I substituted for the bass viol string an electric tuning fork that gave a tone of 128 vibrations per second. The fork was so placed that its base could by a slight movement be brought into contract with the sounding-board and thus, without jar or disturbance to the aquarium, the sound could be delivered to the contained water.

On testing fishes under these conditions, it was found that the earless ones never responded to the tones from the tuning fork, while those with ears very usually did respond. I, therefore, believe that I am entirely justified in drawing the final conclusion that the ears of the killifish are stimulated by sound-waves, that is, that this fish hears. It will be recalled that in the experiments with the bass viol string the earless fishes responded eighteen times in the hundred trials. I believe that the tuning fork experiments, in which no earless fishes responded, make it probable that these eighteen responses were due not to the stimulating effect of sound on the skin of the fishes, as might be inferred, but to some other cause such as the trembling of the whole aquarium. I do not wish to imply, however, that the skin of a fish may not be stimulated by sound.

Although the conclusion that a fish hears is directly contrary to that arrived at by Lee, it is not at all necessary to suppose that the observations of this investigator and those of Kreidl should be regarded as incorrect. Neither Kreidl nor Lee worked on the killifish and the ears in this species may be different from those in the fishes studied by these two investigators. In fact, in my own work I tried on the smooth dogfish (Mustelus canis) the same experiments as those that I have just described for the killifish, but without obtaining the least evidence of hearing in this species. I am, therefore, quite prepared to believe that there are fishes in which the sense of hearing is undeveloped, and these may have been the very forms with which Kreidl and Lee worked; but that there are fishes that do hear I feel perfectly certain.

The ear is related to other sense organs in a way unusually well seen in fishes, and before closing I wish to call attention briefly to this aspect of the subject. The sense organs concerned are the skin and the lateral-line organs. Everyone is familiar with the skin as an organ of touch, but the lateral-line organs are less generally known for at least one obvious reason, namely, that man possesses none. Lateral-line organs occur only in the true aquatic vertebrates, the fishes and the amphibians, and in the latter only in those stages in which the animals inhabit the water. Thus in the frog, lateral-line organs are present while this amphibian is a tadpole, but, as soon as it takes on the adult form and emerges from the water, these organs disappear. Lateral-line organs, then, are in some way intimately associated with the water habit.

These organs form regular lines on the skin of an amphibian or a fish, though in the latter they are more frequently in grooves in the skin or in tubes that lie immediately under the skin and whose courses are indicated by numerous openings, the lateral-line pores. In many fishes three such lines of pores can be recognized on the side of the head, one above the eye, a second immediately below the eye, and a third on the lower jaw. From the union of these three near the back of the head, a fourth line passes posteriorly along the side of the fish, the lateral line, from which the whole system takes its name.

Modern embryology has shown that the ear is closely related to the lateral-line system. The deep situation of the ear-sac at first sight seems to preclude this, but the ear-sac does not form in this situation. In fishes, as in higher vertebrates, this sac forms as a pocket of skin pushed into the head as it were from the outer surface and in fishes it can be shown that the skin which is thus infolded is a portion of the lateral-line system. After the sac has been formed, it sinks into the deeper part of the head, generally loses its connection with the outer skin, and gradually takes on its final complicated shape by producing semicircular canals, etc. Thus the internal ear may be regarded as a modified part of the lateral-line system. This system in turn develops from the skin, and when its organs lie in tubes, as they do in most fishes, the tubes are formed from groove-like depressions of the skin. Thus the lateral-line organs are specialized sense organs from the skin.

These facts suggest at once interesting relations between the three sets of organs mentioned; for, as the lateral-line organs may be regarded as derived from the undifferentiated sense organs of the skin, so the ear may be conceived to have been derived from the lateral-line organs. Thus, we are dealing with what may be called three generations of sense organs: the skin representing the first generation, and giving rise to the lateral-line organs, the second, which in turn produce the third, the ears.

This view of the relations of these three sets of organs accords well with what I have been able to make out about their functions in the killifish. It has already been shown that only such fishes as have their ears intact respond to the sound of a tuning fork. Consequently we may conclude that such sounds do not stimulate either the lateral-line organs or the skin, but that they are a stimulus appropriate to the ear.

The lateral-line organs can also be shown to possess a stimulus peculiar to themselves. These organs were originally supposed to be merely slime glands for the production of the slimy covering so characteristic of the skins of fishes. In 1850 Leydig demonstrated their sensory character, and since then they have given rise to much speculation among naturalists. Since they occur in fishes that have the usual five senses, Leydig (1868) regarded them as organs of a sixth sense quite distinct from any that we possess. Schulze (1870) thought they served to detect mass movements of the water as when a current passes over the surface of a fish or the fish swims through the water. Merkel (1880) believed that they were simply organs of touch, and Emery (1880) and P. and F. Sarasin (1887–1890) regarded them as accessory ears. Fuchs (1895) brought forward evidence to show that they were pressure organs, and Richard (1896) believed they were in some manner connected with the production of gas in the swim-bladders of fishes. Bonnier (1896) was of opinion that among other things they oriented the fish in reference to centres of disturbance in the water, and Lee (1898) thought them organs of equilibration. Thus, much difference of opinion prevails as to the supposed function of these organs.

In the killifish the stimulus for the lateral-line organs is easily found. If an aquarium in which a normal fish is sporting is made to undergo a slight inaudible oscillation by some means not visible to the fish, the latter will dart at once to the bottom. This happens even when the oscillation is scarcely perceptible to the observer. After the nerves to the lateral-line organs have been cut, the fish will no longer respond to these slight movements, but will continue sporting about even when the aquarium is made to tremble considerably. The responses obtained from killifishes under these conditions are so invariable that I conclude that their lateral-line organs are stimulated, much as Schulze suspected, by a slight but inaudible movement of the whole mass of water, a movement that is too delicate to stimulate their skins.

The skin I found to be stimulated by the movements of the water in surface waves and in currents. If a fish in which the lateral-line organs have been rendered inoperative swims into a region where surface waves affect it, it will swim downward out of the reach of these, though it does not go to the bottom of the aquarium as a fish with lateral-line organs does. If it is placed in a current of water, it will swim as vigorously against the current as a normal fish will. Thus the skin, though not stimulated by sound from a tuning fork or the slight inaudible trembling of the whole mass of water, is stimulated by currents and by surface waves.

Hence the three sets of sense organs under consideration may be regarded as having slightly different kinds of stimuli: the skin being affected by surface waves and by currents; the lateral-line organs by slight inaudible movements of the whole mass of water; and the ears by the still more delicate vibrations of water particles, sound. These three sets of sense organs, therefore, are not only genetically connected in that they represent so to speak three generations of organs, but their evolution has been toward more and more delicate means of stimulation. From this standpoint the lateral-line organs of the fishes and the amphibians may be said to be delicate organs of touch and even the ear as an organ of hearing may be looked upon as an exquisitely refined apparatus of much this same kind.[1] Hearing, then, is a most delicate form of touching, and the organ of hearing has developed late in the animal series because its processes are not original but are derived from those of the more primitive sense, touch. Many fishes possess at once the complete series of sense organs leading from touch to hearing, and in these animals the activities dependent upon such organs form doubtless a more or less homogeneous whole; but with us touching and hearing are very distinct things, a condition, however, that we can easily understand, for we have lost the intermediate sense, that of the lateral-line organs. Thus the consideration of the sense of hearing in fishes leads us to an understanding of a natural group of sense organs whose genetic connections would never have been suspected had we not been able to investigate them in these primitive aquatic vertebrates, the fishes.

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[1] At first sight it might seem that this view ignored completely the equilibration function of the ear, a function which may be the only one possessed by this organ in some of the lower fishes, but there are no facts so far as I know that prevent one from assuming that the stimulus for the lateral line organs may not be much the same as that for the ear as an equilibration organ and thus this function might indicate a sensory activity somewhat intermediate between that of the lateral line organs and of hearing. At least unless this is shown not to be the case, the equilibration function of the ear offers no real obstacle to the acceptance of the opinion expressed above as to the physiological relations of the skin, lateral line organs, and ear.

Postscript. Since this lecture was prepared Professor Tullberg's interesting paper (1903) on the functions of the ears of fishes has reached me. In this paper it is concluded (p. 20) that the ears of fishes are not organs of equilibration and though they may perhaps be to a certain extent organs of hearing, their original and principal function is to receive stimuli from the movements of the surrounding water, especially from currents. Vibrations probably stimulate particularly the maculæ acusticæ of the utriculus, the sacculus, and the lagena; currents affect especially the cristæ acusticæ of the ampullæ. Thus the ear is held to be an organ directly concerned with the reactions of a fish to a current of water (rheotaxis).

My own experiments have been directed to test the sense of hearing in fishes rather than to ascertain what other functions the ears in these animals may have, but some of my observations bear on the questions raised by Professor Tullberg and I, therefore, call attention to them here. Professor Tullberg believes that the ears of fishes are not concerned with equilibration because the disturbances in the equilibrium of fishes that follow many operations on the ears and that have been taken to indicate this function, sooner or later disappear, and must, therefore, be regarded as shock effects and not due to the loss of a special sense organ. I have observed much the same condition in *Fundulus heteroclitus* as that described by Professor Tullberg in that two or three days after the eighth nerve has been cut the fishes often swim quite normally. If, however, they are made to swim very rapidly, they invariably lose all orientation and move in irregular circles and spirals. I, therefore, believe that the loss of the ear may have a *lasting* effect on the orientation of fishes in certain forms of locomotion, for these irregular movements were always observable in earless Fundulus even up to the time of death, in some instances six weeks after the cutting of the eighth nerve. The apparent recovery after the operation I attribute to the increased use of the eye as an organ for orientation and though this is an assumption on my part, it is one well supported by evidence from the invertebrates, and, until it is shown to be false for fishes, it seems to me to make Professor Tullberg's conclusion that the fish ear has nothing to do with equilibration at least premature.

My observations on the lateral line organs of Fundulus (Parker, 1903, pp. 59–62) are in entire agreement with those of Professor Tullberg (1903, pp. 8, 15) on these organs in other fishes in that I have found no evidence that these organs are essential to the normal swimming of a fish against a current. But since in Fundulus I could not persuade myself that the ear was not in some degree connected with equilibration, I was unable to devise a satisfactory experiment that would test in the absence of the ear, other organs of sense, such as the skin, that might be stimulated by water-currents. The only evidence I was able to obtain was that when fishes whose spinal cords and lateral-line nerves had been cut several days before, were held by the head near a gentle current of water the tails bent toward the current even though the action of the current on a cordless fish similarly held was to force the tail in the opposite direction. I am, therefore, entirely certain that the skin of the trunk of *Fundulus heteroclitus* is stimulated by water-currents, though I cannot say that these may not also stimulate the ears. I must confess, however, that Professor Tullberg's evidence (1903, pp. 11, 14,) on this point, namely, that after cutting both horizontal semicircular canals the fish no longer orients to a current, does not seem to me wholly conclusive, for this operation may bring about the observed condition by a slight interference with the equilibration function of the ear. In Fundulus swimming against a current of water is dependent in my opinion upon at least two factors: first, the retention of the normal position of the fish which is chiefly accomplished, I believe, by means of the ears as equilibration organs ,and, secondly, directive locomotion which is dependent upon the stimulating effect of the current on the skin of the fish. Under these conditions an interference with the ear might well give rise to a loss of rheotaxis though the primary stimulus for this form of response might be received by the skin. Since the evidence that I have gathered from Fundulus seems to me to show conclusively that this fish uses the ears as organs of equilibration and since the skin in this species is stimulated by water-currents, I believe that the rheotaxis of this species probably is primarily dependent upon the skin, though it may be profoundly influenced by impulses originating in the ear either through a disturbance of equilibrium, as I have already suggested, or possibly directly, as Professor Tullberg believes.

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